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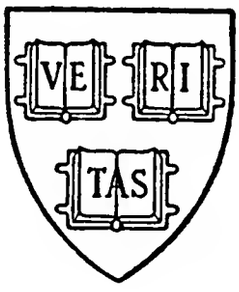

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TRANSACTIONS OF THE SOCIETY FOR BRITISH ENTOMOLOGY

VOL. 7. 29TH JANUARY, 1941. PART 4.

THE CHARACTERS OF THE FEMALE AND DISTRIBUTION IN BRITAIN OF *POMPILUS TRIVIALIS* DAHLB., *UNGUICULARIS* THOMS., AND *WESMAELI* THOMS. (HYMENOPTERA: POMPILIDAE).

By G. M. SPOONER, M.A.

INTRODUCTION.

The females of related species in the family Pompilidae (Psammocharidae) are often notoriously difficult to separate. Specific differences are apt to be both small and not clear cut. While for the comparatively small number of recognized British species characters are known by which the female can be determined with more or less certainty, there yet remains one outstanding exception—the three related 'red-bodied' *Pompilus trivialis* Dahlb. (*gibbus* auctt.), *unguicularis* Thoms. and *wesmaeli* Thoms.

The males of these three species have for long been recognized by well-marked characters in the apical sternite, which have been adequately described and figured, and which have never presented any special difficulty to Hymenopterists. It has been quite otherwise with the females, and attempts at separating them have led to considerable confusion. Since many more females than males are taken by collectors, this circumstance has proved an unfortunate handicap in the study of the distribution and habits of the species. A few years ago, largely through the instigation of Dr. R. C. L. Perkins, F.R.S. (which in effect amounted to a challenge!), I began to examine the problem afresh, and, as a result of investigations carried out since then, am now able to present some definite conclusions.

At an early stage, from the examination of specimens collected in Dorset and a considerable series in Dr. Perkins'

collection,* I had arrived at the probable correct diagnosis of *trivialis* and *unguicularis* (since confirmed), but, as this contradicted existing authorities, wished to obtain adequate confirmatory evidence from inspection of a wider range of material and by capture of specimens *in coitu*. This last aim has not been achieved, but the data accumulated has proved sufficient for the purpose. Various opportunities for examining British material have been taken as they arose, and now, altogether, the number of British specimens examined amounts to the following: *P. trivialis*, 185 ♂♂, 443 ♀♀; *P. unguicularis*, 51 ♂♂, 105 ♀♀; *P. wesmaeli*, 31 ♂♂, 17 ♀♀.

Access to this range of material has only been possible through the facilities I have been granted for examining the contents of collections, and the fact that in most cases the specimens were forwarded to me, or lent me to examine at leisure. I wish to express my indebtedness to all those who have been concerned in giving me this help. Dr. R. C. L. Perkins, Dr. O. W. Richards, Mr. H. M. Hallett, Rev. A. Thornley, and Mr. K. M. Guichard have lent me the specimens in their collections; and Dr. C. D. Day, Dr. F. H. Haines, Mr. A. H. Hamm, and Mr. O. H. Latter have permitted me to examine theirs. Mr. G. J. Kerrich has forwarded to me the material in the collections of the Cambridge and Manchester Museums, and Mr. Hallett that in the Cardiff Museum. The collections in the British Museum, Oxford University Museum (where facilities were kindly granted by Prof. G. Hale Carpenter and Dr. B. M. Hobby), Norwich Museum, and Charterhouse School Museum have been examined. Specimens have also been sent by the late Mr. H. P. Jones. I have further to thank Dr. Perkins, whose readiness to help has been greatly appreciated, for some valued opinions and much interesting information; and Dr. Richards for reading the manuscript.

The problem presented involved not only demonstrating the extent to which specific forms could be distinguished in the female sex, but also, if forms were distinguished, to associate these with the males to which they correctly belonged. As it happened, two main types of female were soon recognized, and later a third was separated from one of them. How far these forms are absolutely separable can be seen from the systematic section of this paper (pp. 89-101). It remains to give the evidence on which they are assigned to the respective species.

In some parts of Britain only a single species, namely *trivialis*, is known to occur. Thus a long series from S. Devon contained only *trivialis* males: the accompanying females all belonged to one type, which could scarcely be other than the same species. Considerable series from Cornwall and Gloucester-

* This has since been transferred to the Oxford University Museum, where it has recently been re-examined.

shire, and several small series from various other districts, also contained only *trivialis* males and the same single form of female. The typical characteristics of the female of *trivialis* were thus established, and a useful impression of its range of variation obtained. When next attention was turned to certain districts where both *trivialis* and *unguicularis* males occurred, *e.g.* heaths in S.E. Dorset and W. Surrey, sandhills in Glamorgan, etc., two forms of the female could be recognized, one already known to be *trivialis,* and the other evidently to be assigned to *unguicularis*. The whole evidence both from regional distribution (see p. 103) and from habitat distribution within a given region (see p. 108) supported this conclusion.

The evidence from distribution is confirmed by whatever taxonomic evidence can be obtained from comparing the two males. These show no constant specific differences, apart from the diagnostic genitalia and apical sternite (Fig. 1) ; but comparison of a series of each has revealed average differences in four characters, all of which are similarly shown, but with clearer differentiation, by the forms of females which had been associated with them.

The separation of the female of the rare *wesmaeli* was less easy. In all localities from which the males are known, both the other species occur. In the earlier examination of the females of the group, no obvious third type could be distinguished. The species was evidently very close either to *trivialis* or *unguicularis*. From the description of *wesmaeli* in Haupt (1927), and from the fact that the male genitalia are very similar, it was inferred that *unguicularis* was the close relative. Examination of specimens from the South Haven Peninsula, Dorset, where more males of *wesmaeli* were taken than of the other two species together, strengthened this view. It was, in fact, from this material that the first indications of the distinguishing characters of the *wesmaeli* female were obtained, from clues provided by wing-venation characters of the male. A third type of female was thus found separable from *unguicularis,* and a re-examination of *unguicularis*-type females disclosed a few more specimens from other localities. The distribution of the twenty-odd females seen fits well with the known distribution of the males.

During the course of establishing and confirming the distinctions between the three species, a number of characters were critically examined and detailed information on them accumulated. The space here devoted to the results of much of this work seems justified on the grounds that some of the characters, including those of which the variation was measured, figure prominently throughout the descriptions of European species, and are of a type which has generally to be relied on in all sections of the family. Distinctions have often to be finely drawn, with questionable justification. At the present state of

our knowledge any information on the degree of variability of these characters within a species may be considered useful.

One possible limitation of the contents of this paper must be noticed. The continental material I have seen is so scanty that I have omitted all reference to it. The systematic data thus

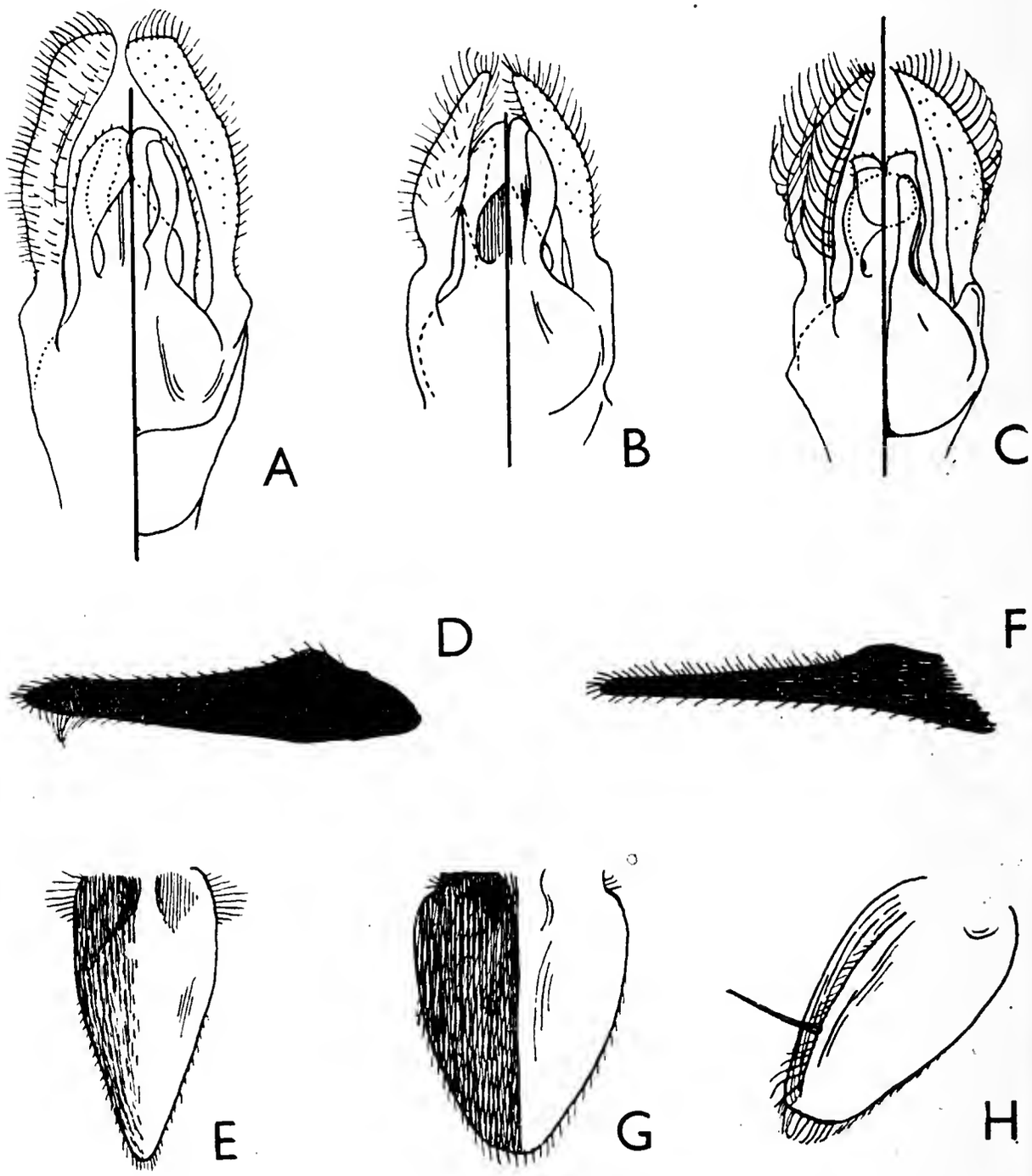
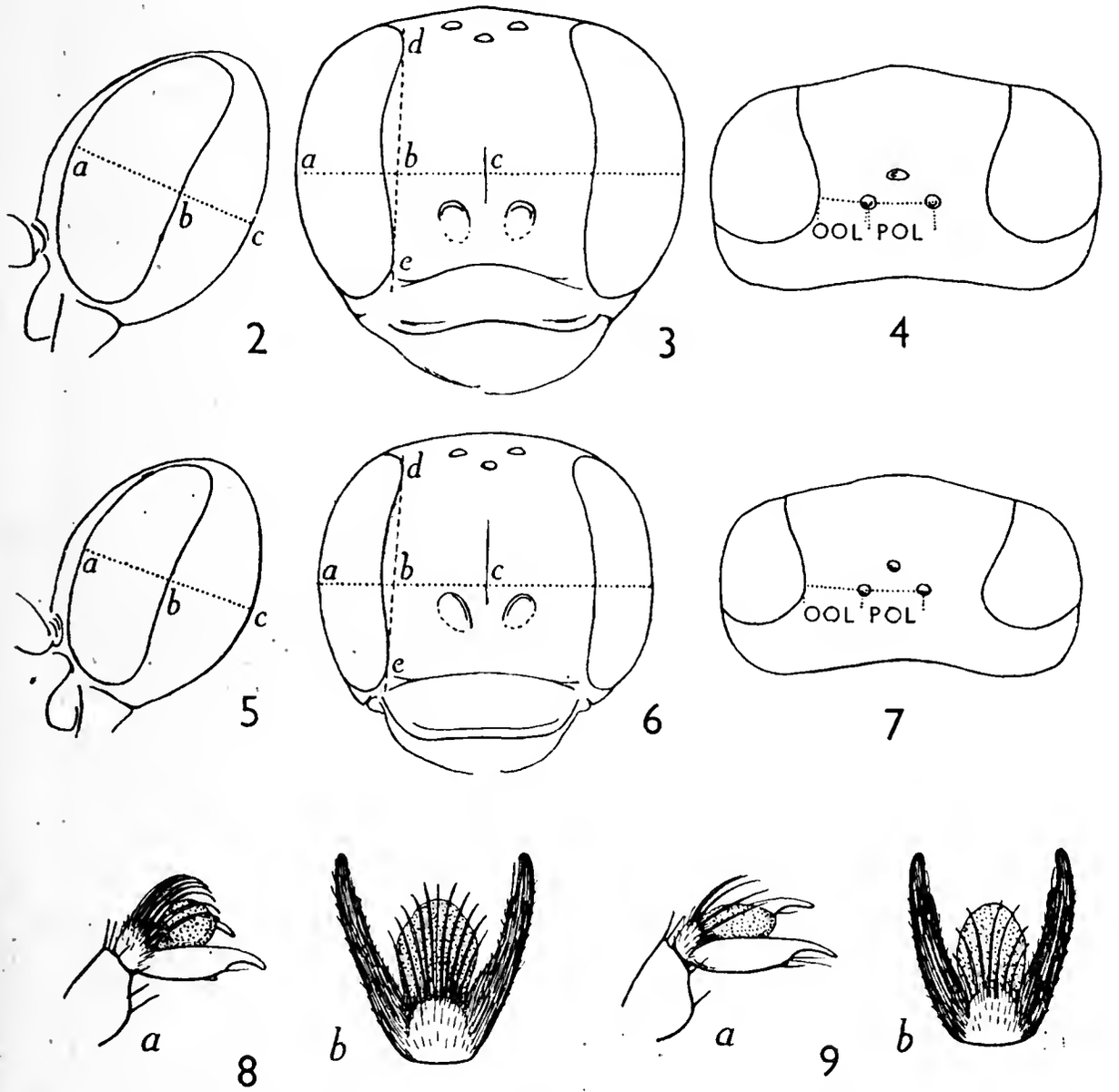


FIG. 1.—Genitalia of (*a*) *Pompilus trivialis*, (*b*) *P. unguicularis*, (*c*) *P. wesmaeli*. Apical sternite of *P. trivialis* (*d*) lateral profile and (*e*) ventral view; *do.* of *P. unguicularis* (*f*) lateral profile and (*g*) ventral view; *do.* of *P. wesmaeli* (*h*) latero-ventral view.

apply to British populations only : it is possible that the species may show somewhat different trends of variation in other parts of their range, and be less distinguishable on the characters by which they can be determined in the British Isles. But I have no special grounds for believing that this is probable.

Specific Distinctions in the Female.

A number of characters have been found to show specific differences, particularly when *trivialis* is contrasted with the other two species. But, as Perkins (1920) suggested, there is probably no one single difference which can be relied on alone. Some, in the typical condition, are fairly well marked, but the variation within each species is sufficient for the occasional



Figs. 2, 3, and 4.—*Pompilus trivialis,* outline of head, in (2) lateral view, (3) frontal view, and (4) vertical view. Figs. 5, 6, and 7.—*P. unguicularis,* outline of head, as above. Fig. 8.—*P. trivialis,* claw and pulvillus, (*a*) oblique view, (*b*) dorsal view. Fig. 9.—*P. unguicularis,* claw and pulvillus, as above. *Note.*—In the outlines of the head scattered setae are omitted. For other lettering see text.

production of doubtful intermediates, while others which may possibly be diagnostic are small and require careful comparison. The determination of a single specimen depends, in principle, on the balance of several characters. In practice, however, this does not involve any laborious assessment, as there are several characters which show but little overlapping variation, and rarely is more than one of them (if any) doubtful in a single specimen.

The distinguishing characters of the species are conveniently listed at this point. Necessary explanations, with some biometric data, are given subsequently. The clearest line of demarcation is that which separates *trivialis* from the other two species.

P. trivialis ♀	*P. unguicularis* and *wesmaeli* ♀
In side view of the head, the central width of the eye typically 1½ to 1¾ that of the temple (average ratio E′ : T = 5 : 3) (Fig. 2).	In side view of the head, the central width of the eye typically 1 to 1¼ that of the temple (average ratio E′ : T = 9 : 8) (Fig. 5).
In front view of the head, the eye occupies about half the area on each side of the whole face. (In Fig. 3 the average ratio of *ab* : *bc* = 1.)	In front view of the head, the area occupied by the eye is clearly less than half that of the whole face on each side. (In Fig. 6 the average ratio of *ab* : *bc* = 3 : 4.)
In vertical view of the head, the posterior ocelli are clearly more widely separated than the distance between one of them and the margin of the neighbouring eye (average ratio POL : OOL = 4 : 3) (Fig. 4).	Distance between the posterior ocelli subequal to that between one of them and the margin of the neighbouring eye (for *unguicularis*, average ratio POL : OOL = 18 : 17, for *wesmaeli* somewhat higher) (Fig. 7).
Propodaeum laterally with evident scattered hairs.	Propodaeum laterally either without hairs, or, if any are present, they are very sparse, short, and fine, and scarcely noticeable.
Claws stouter; pulvillar spines stronger, more numerous, extending well beyond the end of the pulvillus, and unless abraded forming a regular comb (Fig. 8).	Claws rather smaller; pulvillar spines weaker, fewer, and shorter (Fig. 9).
Clypeus anterior margin with a shallow, but distinct, central emargination; apical brim not continuous, almost entirely effaced centrally (Fig. 3).	Clypeus anterior margin with a continuous narrow raised brim, its contour straight or forming a gentle uninterrupted curve (*unguicularis*), or feebly emarginate in the centre (*wesmaeli*) (Fig. 6).

Third antennal segment, in dorsal view, typically slightly longer than the first two segments together.	Third antennal segment equal to, sometimes rather shorter than, the combined length of the first two.
Propodaeum with microscopic surface rugulosity uniformly strong.*	Surface sculpture of propodaeum more obsolete. In *unguicularis* it is very much effaced, giving the surface a distinctly smooth appearance, clearly differing from *trivialis*. In *wesmaeli* it is less effaced, representing an intermediate condition.
Postnotum of variable median width, on average $\frac{3}{4}$ of that of the postscutellum, but sometimes little over a half, and sometimes, on the other hand, fully equal to it.	In *unguicularis* median width of postnotum less variable, $\frac{1}{2}$ to $\frac{2}{3}$ that of the postscutellum. (In *wesmaeli* apparently on average wider.)

The differences between *unguicularis* and *wesmaeli* are fewer, and, as far as has been ascertained from the limited number of specimens of the latter available, are as follows. The wing-venation characters are shown by both sexes, though in the male these are more variable and the average difference not so great.

P. unguicularis ♀	*P. wesmaeli* ♀
In the anterior wing, the 4th abscissa of the median vein considerably longer than the 3rd. (These two veins form the posterior boundary of the 2nd median cell.) (Fig. 10).	2nd median cell less elongate : the two veins which form its posterior boundary—the 3rd and 4th abscissa of the median vein — approximately equal in length and similar in shape (Fig. 11).
The apical area of the anterior wing (*i.e.* the area lying beyond the limits of the radial, cubital and median cells) is narrower : the 2nd recurrent nervure clearly further from the basal nervure than from the wing margin. (For more precise definition see below.)	The apical area of the anterior wing broader : the 2nd recurrent nervure about halfway between the basal nervure and the wing margin. (For more precise definition see below.)

* Clear definition under strong binocular magnification is necessary for this character.

3rd cubital cell usually broad and of greater area than the 2nd, seldom actually less or strongly constricted anteriorly, rarely triangular, never petiolated.

Microscopic sculpture of propodaeum shallow and much effaced.

3rd cubital cell rarely of much greater area than the 2nd, typically much constricted anteriorly, usually triangular, not rarely petiolated.

Microscopic sculpture of propodaeum less effaced, distinct over whole surface, but not so strong as in *trivialis*.

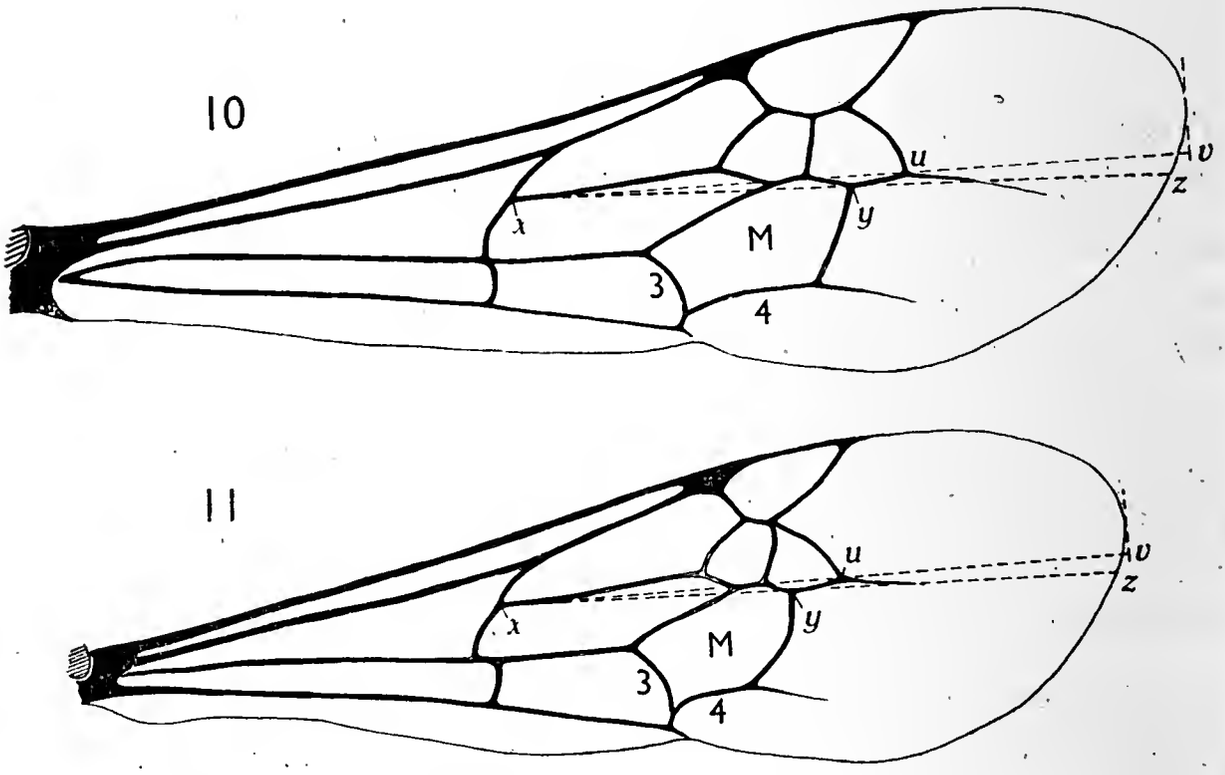


FIG. 10.—*Pompilus unguicularis*, anterior wing.

FIG. 11.—*P. wesmaeli, do.* M: 2nd Median cell. 3 and 4: 3rd and 4th abscissa of Median vein. For other lettering see text.

OBSERVATIONS ON CHARACTERS INVESTIGATED.

Some explanation and comments on the characters which figure in the above lists of specific differences are necessary. In particular, those which involve comparative ratios can scarcely be considered satisfactory unless supported by numerical data. Accordingly measurements have been made with respect to four characters in the first list and two in the second (data given in Appendix I). These serve to demonstrate not only the average difference between the species, but also of the extent to which the characters vary within a single species. They can also be used for testing possible correlation between different characters, or between any character and the size of the specimen (see Appendix II).

Measurements were made under microscope magnification by means of an eye-piece micrometer. All characters (with the natural exception of structures in the median line) were measured on both sides of the body, and the mean of these taken for each specimen. This precaution was found necessary in respect to measurements on the head, since it was not easy to ensure that the profile view being examined was always in exactly the correct plane. Any discrepancy so resulting was eliminated if both sides were measured with the insect in the same position on its stage. In addition, this procedure seemed advisable since it may be considered to give a truer picture of the condition shown by the specimen. In general, however, any differences between the right and left side of the body were found to be small.

The characters are dealt with in the order in which they appear above.

Width of eye compared with that of temple.

The head, in side view, is oval and somewhere in the middle attains a maximum width. At this point (line *ac* in Figs. 2 and 5) the width of the eye, *ab*, and of the temple, *bc*, were respectively measured, and the ratio of *ab* to *bc* calculated. This ratio, designated E′ : T, is evidently equivalent to the 'auge : schläfe' comparison given by Haupt (1927) throughout his monograph. The results are as follows. *P. trivialis*, 48 measured, range 1·28 to 1·99, mean ratio *1·67* with standard deviation of 0·150; *P. unguicularis*, 24 measured, range 0·98 to 1·29 and one 1·41, mean ratio *1·13* with standard deviation of 0·093; *P. wesmaeli*, 6 measured, range 1·07 to 1·24, mean ratio *ca. 1·51*. The two last species are similar in having the eye only slightly wider than the temple, but in *trivialis* it is typically much wider. The overlapping, in the region of 1·30 to 1·40, is small.

Width of eye compared with width of face between the eyes.

The curvature of the eye somewhat complicates straightforward measurement. It was eventually decided to compare the lengths *ab* and *bc* along the horizontal median line *ac* (Figs. 3 and 6), *b* being the point at which *ac* cuts an imaginary line *de*, which connects the margin of the upper and lower lobes of the eye profile. One advantage is that in *trivialis ab* appears to be approximately equal to *bc* : the line *de*, in other words, bisects each side of the face (at least in the middle part). The line of measurement (*ac*) was taken at the broadest part of the front profile of the head. The ratio *bc* to *ab* (designated $\frac{1}{2}$F : E″) was then calculated, with the following results. *P. trivialis*, 48 measured, range 0·90 to 1·17, mean ratio *0·98*, the square root of the variance being 0·067; *P. unguicularis*, 24 measured, range 1·24 to 1·50, mean ratio *1·33*, the square root of the variance

being 0·074; *P. wesmaeli,* 6 measured, range 1·25 to 1·44, mean ratio *ca. 1·32*. The distributions about the mean are far from normal. Again the character is similar in *unguicularis* and *wesmaeli,* which have a markedly wider face (or narrower eye) than *trivialis*. It may be noted that no actual overlap was found.

Spacing of the posterior ocelli (Figs. 4 and 7).

The distance between the mid-points of the two posterior ocelli (POL), and the shortest distance between the mid-point of one of them and the margin of the neighbouring eye (OOL), are the two measurements of which the ratio is taken. This ratio, POL : OOL, is equivalent to one much used by Haupt. In *P. trivialis,* owing at least partly to the fact that the eyes are somewhat more closely approximated towards the vertex, POL is decidedly greater than OOL: of 48 measured, range 1·18 to 1·55, mean ratio *1·33* with standard deviation of 0·079. In *P. unguicularis* the two are subequal: of 24 measured, range 1·00 to 1·12 and one 1·22, mean ratio *1·06* with standard deviation of 0·050. In *P. wesmaeli* the difference from *trivialis* does not appear to be so great: of 6 measured, range 1·06 to 1·21, mean ratio *ca. 1·15*. Between the first two species there is only very slight overlap.

It may be noted that the above three characters, taken together, imply that the surface area of the eye, relative to that of the whole head, is greater in *trivialis* than in the other two species. If this area could be conveniently measured it would evidently provide a more absolute distinction than any single one of the three ratios calculated, since the variations of these show no marked intra-specific correlation.

Propodaeal hairs.

The propodaeum, though naked in general appearance, actually bears two types of hairs. There is, in the first place, the microscopic tomentum, uniformly spread over the surface when the specimen is fresh, but easily abraded. Quite distinct from the minute hairs comprising this, are hairs which rise from the surface, and which even if short and fine are visible in a profile view. These hairs are confined to the sides of the propodaeum. In a species allied to the three considered here, namely *P. consobrinus* Dahlb., they are comparatively dense, so that the propodaeum laterally is quite noticeably hairy. In *P. trivialis* these hairs are by no means altogether absent, but always a larger or smaller number occur, of varying length and stoutness, sparsely scattered, but readily seen if the lateral slope of the propodaeum is viewed in profile. In the other two species either these hairs are lacking, or, if they are present, they are very few in number, and very short and fine, so that they scarcely show under moderate magnification. In badly preserved or much

abraded specimens there is apt to be loss of, or damage to, the propodaeal hairs, but otherwise only very exceptionally have specimens been seen which were at all intermediate or 'doubtful' as regards this character.

Stoutness of claws and pulvillar spines.

Figs. 8 and 9 show the typical forms of the claws and pulvilli in *trivialis* as contrasted with *unguicularis* and *wesmaeli,* stronger in the first and weaker in the last two. Some variation, however, occurs within each species, and an indication of heterogonic development—that is, the larger individuals tend to have relatively stouter claws and longer pulvillar spines. The value of this character is also somewhat decreased by the susceptibility of the claws to the effects of abrasion : the fine pulvillar spines especially appear to be easily lost or broken. Usually, however, at least one of the legs escapes serious damage.

Form of apical border of clypeus.

In *trivialis* typically the apical margin of the clypeus is weakly, but distinctly, emarginate in the centre (Fig. 3). Further, if any apical brim is evident, it is much interrupted in the centre, if not entirely obliterated. *P. unguicularis* (Fig. 6) and *wesmaeli* both show a continuous, rather shining, narrow apical brim, which centrally is not interrupted. In addition, *unguicularis* has the apical margin more or less straight, or forming a gentle uninterrupted curve, according to the angle from which it is viewed. It appears, however, that in *wesmaeli* the apical contour is typically weakly emarginate, though less than in *trivialis*. There is probably a real difference between the average conditions of *unguicularis* and *wesmaeli,* but the character can scarcely be recommended for purposes of separating the species. That between *unguicularis* and *trivialis* is more definite, and here there is scarcely any intergrading.

Length of third antennal segment.

The third antennal segment tends to be somewhat longer and perhaps slenderer in *trivialis* than in the other two species. In the former it is normally a little longer than the combined length of the first two segments, whereas in the others it is equal to it or somewhat shorter. Though this difference is of a small order, measurements would probably show no greater intergrading than in the measured head characters. Careful comparison shows that the males also exhibit a tendency towards the same difference*; but, as with the other characters in this sex, the species intergrade.

* The third joint is short in this sex, and is most conveniently compared with the fourth joint, to which it is approximately equal; but in *trivialis* it tends to be slightly longer, and in the other two to be shorter.

Surface sculpture of propodaeum.

Under a strong magnification the difference between *trivialis* and *unguicularis* is quite distinct and appears to be absolute. In the former the rugulosity is even and firm; in the latter it is very much effaced, so that the surface appears almost smooth. *P. wesmaeli* occupies an intermediate position, but the difference from *unguicularis*, as well as from *trivialis*, was sufficiently noticeable in those specimens which have been examined. In the male sex, the propodaeum is, on the average, rougher in *trivialis* than in *unguicularis*.

Width of postnotum.

The relative width (strictly speaking the 'length') of the postnotum in the central line (*Pn*), compared with that of the postscutellum (*Ps*), is sometimes of systematic value among the Pompilidae. An average difference was suspected. The results of measurements are given as an example of a clear statistical difference in a character which shows overlapping variation. The ratios calculated (*Pn*/*Ps*) range between 0·50 and 1·15 (Table V). Whereas *trivialis* occupies nearly the whole of this range (0·55 to 1·15, in 48 measured), *unguicularis* only varies between 0·50 and 0·65 (24 measured). The means, respectively, are *0·75*, with standard deviation of 0·100, and *0·57*, with standard deviation of 0·047. The width in *wesmaeli* may be higher than in *unguicularis* (for 6 measured, range 0·6 to 0·7, mean ratio *0·66*). The range of variation in *unguicularis*, as measured by the standard deviation, is thus not quite half that of *trivialis*. In separating these two species it can be said that a postnotum width of $\frac{3}{4}$ or more of that of the postscutellum determines *trivialis* with virtual certainty. Thus two out of three specimens of *trivialis* would be determinable on this character. In the males, also, the postnotum is on the average wider in *trivialis* than in *unguicularis*.

Wing venation characters.

As a general rule among aculeates minor characters affecting the venation of the wings have to be treated with special caution, owing to their liability to variation, as well as to the comparative frequency of aberrations. It is not rarely that obvious differences can be seen in opposite wings of the same insect. Nevertheless some wing-venation characters have proved important in the separation of *unguicularis* and *wesmaeli*, which otherwise in the female sex are doubtfully separable. The clue as to probable significant specific characters was first provided by examination of the males of the three species. With the qualification that in the males the average differences are smaller

and that there is more overlapping variation, such distinctions as were noted were found to apply to both sexes.

In the form of its venation *P. trivialis* occupies a central position from which *unguicularis* and *wesmaeli* vary in opposite directions. The differences between the two latter species are thus greatest, and it is only these that are stressed. It is sufficient to note that the average differences which exist between *trivialis* and each of the other two species indicate yet another point of specific divergence.

Three characters in the anterior wing will be considered separately, but each is clearly connected with a single, perhaps more fundamental, characteristic. This is not easily defined; but an attempt to do so would indicate that in *wesmaeli*, at one extreme, the venation as a whole tends to be foreshortened apically, so that the apical unenclosed area (*i.e.* the area of the wing apical to the boundaries of the radial, cubital, and median cells) appears relatively broad, and the more apical of the cells, particularly the 3rd cubital and 2nd median, relatively narrow. The opposite tendency is shown by *unguicularis*, while *trivialis* is intermediate. Of the three characters considered, one is a measure of the relative width of the apical border at a specified position, one relates to the shape of the 2nd median cell, and the other to the relative size of the 3rd cubital cell. The two latter may be expected to be at least partly correlated with the former, though the fact that *trivialis* is not intermediate to an equal degree in all three shows that they are partly independent.

Dimensions of 2nd median cell.

Attention is particularly directed to the relative length of the more apical of the two veins which form the posterior boundary of the cell — here called the 4th abscissa of the median vein. This may be compared with the other member (3rd abscissa) of the pair, which forms a V-shaped figure (Figs. 10 and 11). In *wesmaeli* the 4th abscissa (apical branch of the V) is no longer, or only very little longer, than the 3rd (distal branch of the V). The bend in the former is more abrupt than in the latter, so that the V is symmetrical. By contrast, in *unguicularis*, the 4th abscissa is decidedly longer than the 3rd, and the bend in it sharper, so that the V is markedly asymmetrical. The typical condition in *trivialis* is exactly intermediate. This character appears to provide a diagnostic distinction between *wesmaeli* and *unguicularis*: all the specimens of these species examined fall into two clearly separable groups. Moreover, *trivialis* can usually be separated from the other two, though overlapping to some extent with each of the others in turn at opposite limits of its variation. The males of *unguicularis* and *wesmaeli* show a tendency to the same difference as described for the females, but

in their case there is overlapping variation (actually the average difference is less and the variation in each species greater).

Width of apical border of forewing.

An attempt was made to check by measurements the eye-judgment that the unenclosed apical border of the anterior wing is significantly broader in *wesmaeli*. At a rough estimation, the second recurrent vein in *wesmaeli* is equidistant between the basal vein and the wing margin (Fig. 11): in *unguicularis*, by contrast, it is appreciably nearer the latter, particularly at its posterior end, the 'veined' area being thus wider than the apical border (Fig. 10). To get standard points for measurement, a straight line was taken from the junction of the cubital vein with the basal vein (x) to the anterior end of the 2nd recurrent vein at its junction with the cubital vein (y), and continued to the wing margin (z). The two sections of the straight line xyz, xy and yz, were measured, and the ratio $xy : yz$ calculated. The results obtained (Table V) may be summarized as follows. The ratio in *unguicularis* (24 measured) was found to range between 0·96 and 1·17, its mean value *1·08*, with standard deviation 0·058. For the six *wesmaeli* measured, the values, as expected, were lower, falling between 0·87 and 0·95 (mean *0·91*). The difference is therefore appreciable, but not sufficient to prevent overlapping, which would certainly be found if more of the second species could be measured. If, however, the size of the specimen is taken into consideration, the difference is more absolute. Unlike any of the ratios considered hitherto, that of $xy : yz$ tends to increase with the size of the specimen, thus indicating heterogonic effects. In Fig. 12 the values of the ratio are plotted against xz — the best available index of size. It will be seen that the *wesmaeli* plots fall well clear of those for *unguicularis*. The change of the value $xy : yz$ with increasing size, and the differences in it between the two species, are indicated in the following table.

Size index*	*P. unguicularis* ♀		*P. wesmaeli* ♀	
(xz)	Number	Mean ratio	Number	Mean ratio
150 ...	4	1·00 ...	—	—
160 ...	5	1·06 ...	1	0·87
170 ...	6	1·085 ...	3	0·91
185 ...	4	1·12 ...	2	0·93
205 ...	4	1·125 ...	—	—
225 ...	1	1·17 ...	—	—

While this measurement may not be the most satisfactory means of expressing the relative broadness of the wing margin of

* In micrometer units of 0·0174 mm.

wesmaeli, it is superior to another ratio similarly calculated — that of *xu* to *uv* (Fig. 10). This ratio shows a comparable difference between the species, as well as increase with size, but both relations are less clear cut than the above. In *trivialis* this character is much as in *unguicularis,* and not strictly intermediate.

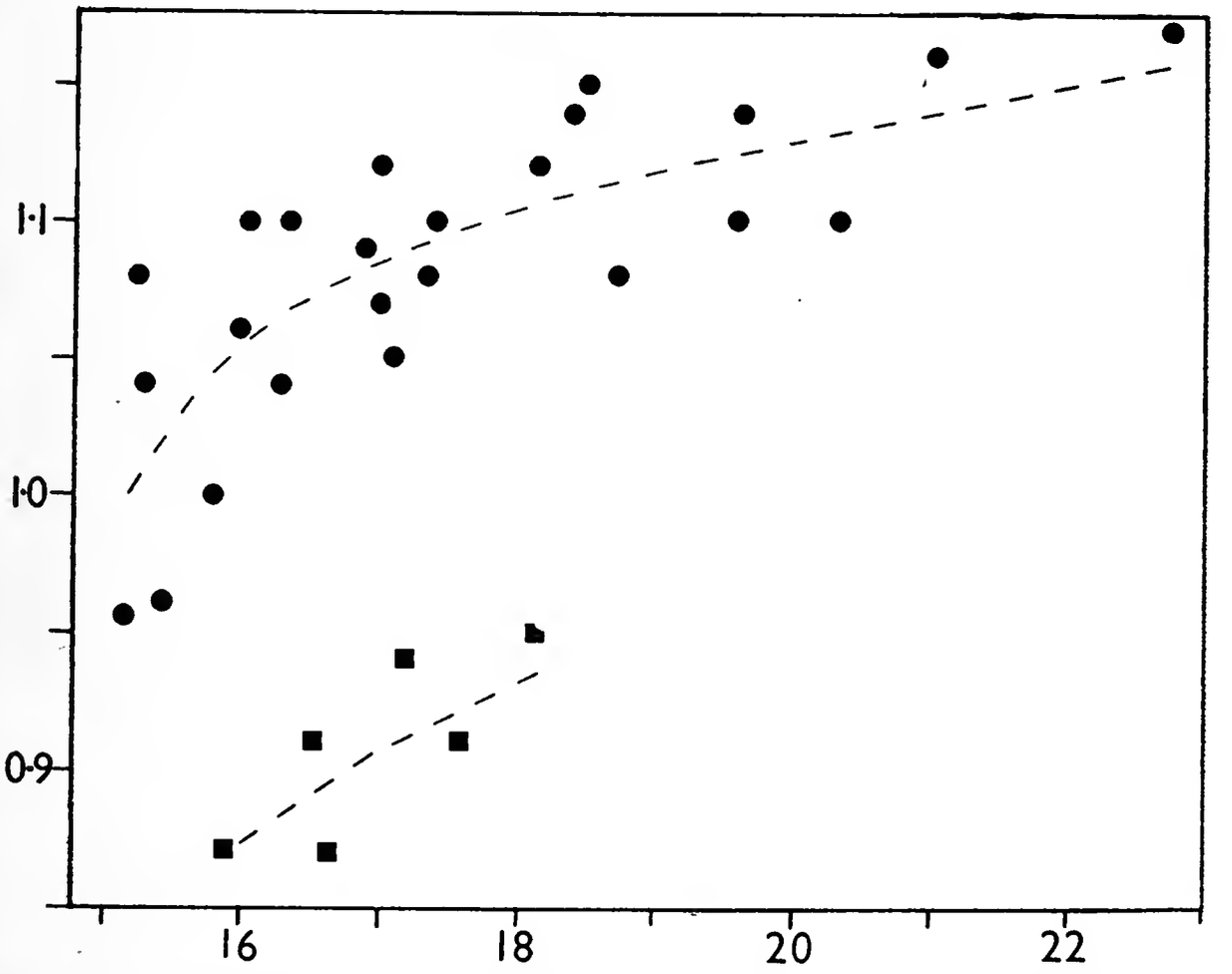


FIG. 12.—*Pompilus unguicularis* (circles) and *P. wesmaeli* (squares): ratio *xy/yz* plotted against *xy+yz,* as index of size. Latter measured in units of 0.174 mm.

Size and shape of 3rd cubital cell (Table I).

In *unguicularis* the most apical of the cubital cells is often broad, usually exceeding the 2nd cubital cell in area, and rarely other than quadrangular. On the other hand, in *wesmaeli* it tends to be much narrowed anteriorly, and so to be of smaller area than the 2nd cell; it is usually triangular in shape, and not rarely petiolated. An intermediate condition is shown by *trivialis*. The accompanying Table summarizes the data of samples of each species, both sexes being treated. The relative size of the 3rd cubital cell is graded into seven categories assessed by eye. The frequency of the quadrangular, triangular, or petiolated condition is also recorded. The condition of both right and left wings on each specimen was taken into account, and when this showed a difference each wing was separately given a value of $\frac{1}{2}$.

TABLE I.

Condition of 3rd cubital cell.

Ttl. — total. *T.* — triangular, not petiolated.
Q. — quadrangular. *P.* — triangular and petiolated.

Size relative to 2nd.	*P. unguicularis* Ttl.	*Q.*	*T.*	*P.*	*P. trivialis* Ttl.	*Q.*	*T.*	*P.*	*P. wesmaeli* Ttl.	*Q.*	*T.*	*P.*
FEMALE												
Much larger ...	10	10	–	–	–	–	–	–	–	–	–	–
Larger ...	19½	19½	–	–	1	1	–	–	–	–	–	–
Slightly larger	21	21	–	–	6	6	–	–	2	1	1	–
Equal	9½	9	½	–	14	13½	½	–	3½	2	1	½
Slightly smaller	4	3	1	–	10	4½	5½	–	2½	–	2	½
Smaller ...	1	–	1	–	10½	2½	8	–	1	–	1	–
Much smaller .	–	–	–	–	2½	–	2	½	1	–	–	1
Total ...	65	62½	2½	–	44	27½	16	½	10	3	5	2
MALE												
Much larger ...	5	5	–	–	1½	1½	–	–	.	–	–	–
Larger ...	9	9	–	–	7	6½	½	–	4	2	–	–
Slightly larger	9½	7½	2	–	2½	2	½	–	3	1	2	–
Equal	4½	4½	–	–	6½	5	1½	–	1	–	1	–
Slightly smaller	½	½	–	–	7	6	1	–	3	–	3	–
Smaller ...	½	–	½	–	11	6½	4½	–	9	–	8	1
Much smaller .	–	–	–	–	3½	1	2	½	2	–	1	1
Total ...	29	26½	2½	–	39	28½	10	½	20	3	15	2

The tabulated results show, in the first place, a very similar state of affairs in both sexes, though the males tend to be more variable; and, secondly, marked average differences between *unguicularis* and *wesmaeli*, as indicated already.

Size.

The size range of *trivialis* ♀ is considerable. The body length varies between 7 and 10½ mm., which is equivalent to a wing expanse of 10·5 to 16 mm. (The latter measurement is the more satisfactory: the body length of specimens with a normally extended abdomen was found to be ⅔ of its value, and can thus be derived if required.) The range of *unguicularis*, 6¼ to 10 mm. body length, and 9½ to 15 mm. wing expanse, is almost as great, but the average length slightly less. The difference between the average size of the two species is indicated in the size-index distribution given in Table V, but some 5 per cent. (about one group unit) must be added to the *unguicularis* figures, to allow for the fact that the head-width, used as the index, is

relatively less by about this amount. The six *wesmaeli* females all fall within the lower half of the range of *unguicularis* (7 to 8 mm. body length).

Other characters. Mention should be made of some other characters which were examined because they figure in previous descriptions (for comment on these, see below). The width of the head relative to the body appears, on the average, to be slightly less in *unguicularis* than in *trivialis*; but a small sample measured showed an average difference of only about 5%. The spacing of the ocelli suggests a probable statistical difference: in *unguicularis* the three ocelli form an acute or right-angled triangle, whereas in *trivialis* it is right-angled or obtuse. It seemed possible that the average relative size of the ocelli is less in *unguicularis*. Some measurements were made of the diameter of the anterior ocellus and compared with the width of the face (28 specimens of *trivialis* and 18 of *unguicularis* measured): the results indicate only a small average difference of some 6%. The difference in the average space between the anterior ocellus and one of the posterior ocelli, combined with the diameter of the former, proved to be of the same amount. The density of the hairs on the posterior part of the head and on the pronotum anteriorly, which together protrude into the space between the head and the thorax, appears, on the average, to be greater in *trivialis,* and the hairs longer, than in the other two species; but the hairs are apt to be denser and more conspicuous in robust specimens. Probably, on the average, the hairs on the head are even shorter and sparser in *wesmaeli* than in *unguicularis*.

Comments on Previous Descriptions.

C. G. Thompson (1870) in Sweden was the first to introduce *unguicularis* and *wesmaeli* as species distinct from *trivialis*. His descriptions (1870, 1874), however, are short, and define only the male at all clearly. The female which he called *unguicularis* is described as having longer pulvillar spines, the head rather more hairy, and attaining larger size, than *trivialis*. This suggests that, in so far as he correctly segregated the females, he assigned them to the wrong male. His *P. wesmaeli* ♀, which is given as most resembling *trivialis,* was probably, as far as it is possible to judge from the characters given, correctly identified.

In Britain, E. Saunders (1896) attempted to follow Thomson and to some extent appreciated further differences between the two females belonging to one or other of *trivialis* or *unguicularis*. For one type, which he assigns to *unguicularis,* the following characters are given: sides of propodaeum finely pilose, comb of spines between the claws longer and more regular (noted as difficult and unsatisfactory), size generally larger, eyes rather closer together on the vertex, face less convex, and cheeks behind the eyes and pronotum anteriorly more pilose. The other type, assigned to '*gibbus,*' and imperfectly described, lacks pilosity of the sides of the propodaeum, has shorter claws and spines, and, in short, differs in respect to the various characters mentioned above. It will be noted that the first four characters given for the first type are actually specific, not for *unguicularis,* but for *trivialis*. Thus in so far as the two forms of female were

correctly distinguished they were still placed under the wrong species. Examination of Saunders' collection (coll. Brit. Mus.) showed, however, that the segregation of the two forms was imperfect. Though under '*unguicularis*' were placed a number (33) of the more robust specimens with obvious (as it proves) *trivialis* characters, yet under '*gibbus*' were found 39 specimens of *trivialis* (including Saunders' 'type' of the species) and 26 of *unguicularis*, with the addition of 3 *wesmaeli*.

Saunders was unable to determine the female of *wesmaeli*. The specimens he assigned to this species were found to include one specimen correctly identified, and five others, including his 'type,' all *unguicularis*.

Perkins (1920) fully recognized that previous attempts at diagnosing the females of the three species were unsatisfactory. In the new key he gives for the females of British Psammocharidae (Pompilidae) no attempt is made to distinguish between them, and the opinion is expressed that they are probably not determinable on any character with certainty.

For descriptions applying to Europe as a whole, the most recent and complete are those given in Haupt's monograph (1927). Of the eight European species, of which four are British, in this section of the genus *Pompilus* (*Psammochares* in Haupt), only three concern us here. *P. unguicularis* (*loc. cit.*, p. 201) and *P. gibbus* (= *trivialis*) (p. 204), both widely spread on the continent, are recognized to be very similar in the female. The former species is described in some detail, and the latter simply by the ways in which it differs. On the whole the two descriptions are found to fit closely with the two main forms of female which, as described above, have been distinguished in Britain—with one critical reservation—that the female of *unguicularis* has to be transposed to *gibbus*, and *vice versa*. Thomson's original error has thus been perpetuated more systematically on the continent. It seems very curious that this error should have remained undetected.

If Haupt's description of female *unguicularis* be applied to *trivialis*, it will be seen that nearly all the character differences dealt with above are brought in. No indication, however, is given as to which characters are to be regarded as relatively stable or diagnostic and which are liable to appreciable deviations; and (assuming the British population is not more variable than elsewhere) various qualifications would be necessary to make the description really adequate. The description of *gibbus* female, transposed to *unguicularis*, is not seriously at fault as far as it goes, but it requires certain qualifications and can be supplemented with additional characters brought to notice above.

The description of *wesmaeli* female (*loc. cit.*, p. 206) is applicable to British specimens, but it gives no satisfactory characters by which the species can be separated from *unguicularis* (*i.e.* Haupt's *gibbus* female). The character used in the key, regarding the emargination of the clypeus, is probably not altogether invalid, but the difference is only an average one, and is in any case too slight to be of practical use. The distinctions in the wing venation, brought to notice above, are not recognized.

Distribution in Britain.

Pompilus trivialis Dahlb.

This is the most plentiful and widely distributed of the three species, ranging into the north Highlands of Scotland, and apparently widely spread in at least the coastal districts of Ireland. Over most of this range it is evidently a common species, frequenting various kinds of exposures of bare ground on a variety of light soils. But it is not at all partial to heavy clays.

From the southern half of England I have seen specimens taken in the following vice-counties: Scilly Is., W. Cornwall, E. Cornwall, S. Devon, N. Devon, N. Somerset, N. Wilts, Dorset, I. of Wight, S. Hants, W. Sussex, E. Sussex, W. Kent, E. Kent, Surrey, N. Essex, Middlesex, Berks., Oxon., Bucks., E. Suffolk, W. Suffolk, E. Norfolk, Cambs., Hunts., Northants., W. Gloucs., and Hereford. Previous reliable records, based on captures of the male, existed for several of these vice-counties. The records for W. Norfolk (Atmore, 1909)—2 ♀♀ '*unguicularis*' from King's Lynn (the determination presumably based on Saunders and so applying to this species)—Herts (Palmer, 1924), and Worcester (Bradley, 1900) remain to be confirmed.

In Wales, Hallett (1928) records the species as 'common inland and on sandhills' in Glamorgan: specimens of both sexes in his collection from various localities have been confirmed. In coll. E. B. Nevinson (Oxford Univ. Mus.) are the following specimens taken by this collector in Carnarvon: Deganwy, 1 ♀; Criccieth, 3 ♂♂ and 10 ♀♀; Abersoch, 1 ♀; and in Merioneth: Towyn, 1 ♀.

For the northern half of England, I have seen only the following specimens. Cheshire: Delamere, 1 ♀ (Britten) (coll. Manchester Mus.). Notts: Bramcote, 1 ♀ (Jones) (coll. Wollaton Mus.). Yorks, M.W.: Roundhay, 2 ♀♀, Collingham, 2 ♀♀ (Bradley) (coll. R. C. L. Perkins). Yorks, N.E.: Whitby, 1 ♂ and 1 ♀ (coll. Brit. Mus.). Yorks, N.W.: Wensley Dale, 1 ♂ (coll. O. W. Richards). The male is also recorded from N. Lincs., Skegness (Thornley, 1901). Other published records do not specifically mention the male—Notts., several localities (Carr, 1916, 1935); Cheshire and S. Lancs., 'common' (W.

Gardner, 1901)*; Yorks, S.W. and S.E., various localities, (Butterfield and Fordham, 1930); and Cumberland, 1 ♀ (Routledge, 1933) — and so require confirmation, though it is highly probable that this species is involved in most cases.

The Scottish material examined includes the following:— Easterness: Nethy Bridge, 1 ♂ (D. Sharp) (coll. Camb. Mus.). W. Ross: Aultgrishin, 1 ♂ (Spooner, 1937). Sutherland, E.: Golspie, 1 ♀ (Yerbury) (coll. Brit. Mus., recorded by Saunders, 1900, as *unguicularis*). Several of both sexes, seen by Saunders, were taken at Comrie, S. Perths. (Carter, 1901); and both sexes are recorded from Roxborough (Clark, 1924). It may be noted that the species is so far unknown from any of the Hebrides or Northern Isles, and it has still to be discovered whether it reaches the extreme north coast.

This is the only species yet known to occur in Ireland, the following specimens having been confirmed: — Dublin: Glencree, 1 ♂; Portrane, 1 ♂, 2 ♀♀; N. and S. Strand Rush, 2 ♂♂, 3 ♀♀ (Stelfox) (colls. R. C. L. Perkins and Manchester Mus.). Wicklow: 1 ♂ (coll. R.C.L.P.). S. Kerry: Waterville, 2 ♀♀ (Yerbury) (coll. Brit. Mus.). Among other vice-counties given by Stelfox (1927), E. Cork is the only one for which the occurrence of the male is recorded, but the species involved in the other cases — W. Cork, Wexford, Meath, Clare, S. Galway, E. and W. Donegal, Louth, and Down — may be assumed to be *trivialis* in absence of contrary evidence.

The species figures amongst the restricted aculeate fauna of outlying islands, but the extent of its range in this direction is very imperfectly known. It occurs in the Isles of Scilly, where it has been taken on Tresco (1 ♂ and 3 ♀♀) and St. Mary's (3 ♀♀) by Dr. O. W. Richards; and apparently also on Lundy Island, if F. Smith's record (Parfitt, 1880) truly refers to one of this group of species. Hallett (*in litt.*) records it from Ramsey Island, Pembroke, but the identification has not been checked. Data from other Welsh and Scottish Isles are lacking. The upper limits of the range of *trivialis* in mountainous districts are also very little known.

P. unguicularis Thoms.

Many past records of this species refer to females only, for which the means of identification have been incorrect (p. 101). It is therefore necessary to give a complete revision of the distribution in Britain, on the basis of the material which has been examined. The vice-counties in which its occurrence has been established are dealt with first.

* But may include *unguicularis*, q.v.

Dorset :—On the Bagshot Sand heaths in the south-east of the county, from Warmwell Heath to Studland, as numerous as *trivialis* : 3 ♀♀ (coll. F. H. Haines), 2 ♀♀ (coll. C. D. Day), 1 ♀ (coll. O. W. Richards), 10 ♂♂ and 20 ♀♀ (coll. G. M. Spooner). Coast east of Weymouth, on sandy strata, 1 ♀ (coll. G.M.S.).

Hants, S. :—New Forest, 3 ♂♂ (Arnold) (colls. R. C. L. Perkins and Camb. Mus.), 2 ♀♀ (Arnold) (colls. R.C.L.P. and E. B. Nevison, Oxford Mus.). Queen's Bower, New Forest, 1 ♀ (coll. A. H. Hamm). Bournemouth, 1 ♀ (Saunders) (coll. Brit. Mus.). Beaulieu Road Station, 1 ♀ (coll. A. H. Hamm). Beaulieu, 1 ♀ (Le Marchant) (coll. Brit. Mus.). Hayling I., 5 ♂♂ and 1 ♀ (Saunders) (colls. Brit. Mus., Norwich Mus., Oxford Mus., and G.M.S.).

Kent, E. : — Deal, 1 ♂, 5 ♀♀ (Saunders) (colls. Brit. Mus. and Norwich Mus.). Deal Sandhills, 9 ♂♂ and 6 ♀♀, 27.v.39 (coll. K. M. Guichard). The record for Herne Bay (Saunders, 1896) should be transferred to *trivialis*.

Surrey :—In the Bagshot Sands district about as frequent as *trivialis* : Chobham, 4 ♂♂ and 11 ♀♀ (Saunders) (coll. Brit. Mus.) ; Woking, 3 ♂♂ and 12 ♀♀ (Saunders) (coll. Brit. Mus.) ; Cobham, 1 ♂ and 3 ♀♀ (Nevinson) (coll. in Oxford Mus.) ; Oxshott, 1 ♂ and 2 ♀♀ (coll. O. W. Richards), 1 ♀ (coll. K. M. Guichard) ; Bagshot, 1 ♂ (coll. O.W.R.) ; W. Byfleet, 1 ♂ (Pagden) (coll. O.W.R.) ; Horsell, 1 ♀ (R. J. Champion) (gen. coll. Oxford Mus.) ; Lower Greensand district : Godalming, 1 ♀ (Latter) (coll. Charterhouse Mus.).

Berks. :—Tubney, 1 ♂ and 4 ♀♀ (coll. A. H. Hamm), 1 ♀ with prey (Oxford Mus. Coll.).

Oxon :—Shotover, 1 ♀ (coll. A. H. Hamm).

Suffolk, W. : — Breck Sands district : Mildenhall, 2 ♀♀ (R.C.L.P.) (coll. Camb. Mus.) ; Barnham, 1 ♀ (Nurse) (coll. Cardiff Mus.) ; Lakenheath Warren, 1 ♀ (Pagden) (coll. O.W.R.). Dr. Perkins states (*in litt.*) he took other specimens in this district, including males, which were not rare.

Glamorgan : — Coast sandhills : Porthcawl, 1 ♂ and 1 ♀ (Yerbury) (coll. Brit. Mus.), 5 ♂♂ and 2 ♀♀ (Hallett) (colls. Cardiff Mus. and R.C.L.P.) ; Llangennith sandhills, 2 ♀♀ ; Kenfig, 3 ♀♀ (Hallett) (coll. Cardiff Mus.) ; Gower, 1 ♀ (P. Harwood) (coll. R.C.L.P.). In carboniferous limestone localities : Sully (Swanbridge), 1 ♂ ; Cwyrt-yr-ala, 2 ♀♀ (Hallett) (coll. Cardiff Mus.). Mr. Hallett (*in litt.*) states he formerly took other males in the Cwyrt-yr-ala and other localities on the same geological formation. The county records given by Hallett (1928) are thus confirmed, and it is seen that the species is by no means confined to the sandhills.

Cheshire: — Wallasey sandhills, 2 ♀♀ (Arnold) (coll. R.C.L.P., Oxford Mus.); Delamere, 1 ♂ (Arnold) (coll. R.C.L.P.).

Lancs., S.: — Coast: Ainsdale, 1 ♀ (Britten) (coll. Manchester Mus.).

[Norfolk, E.:—Unlabelled specimens of a ♂ and ♀ in coll. J. B. Bridgman (coll. Norwich Mus.) are probably from the Norwich district.]

The following vice-counties may be added on authorities accepted as reliable.

Essex, N.: Colchester district (E. Saunders, 1896; W. Harwood, 1903). Glouces., W.: Wotton-under-Edge, a single male taken by V. R. Perkins prior to 1885, determined by Saunders and later confirmed by R. C. L. Perkins (information *in litt.*). It was this capture, Dr. Perkins says, which led to the determination by Saunders of several females of *unguicularis*. Later Dr. Perkins became sceptical of this determination, the characters of the Wotton females, captured then and subsequently, agreeing with those of specimens he took in other localities accompanying *trivialis* males, and which, as has now been established, are properly applicable to that species. Thus the record 'freely in the woods near Wotton about 1885' (Perkins, 1924) applies to females, and is invalid. Altogether I have examined 9 ♂♂ and 22 ♀♀ from Wotton, including specimens taken in 1885, and all are undoubted *trivialis*. (V. R. Perkins' *unguicularis* ♂ unfortunately was not among the specimens surviving in his collection, which is in my possession.) There seems no doubt that, as would be expected, *trivialis* is the prevalent species in this district, and *unguicularis* at most a rarity by comparison.

Clyde Isles: — Arran: King's Cross, 1 ♂, August, 1900 (Dalglish, 1901). This is the only record from Scotland. The occurrence of the species in Sutherland (Saunders, 1900) is based on a ♀ which proves to be *trivialis* (p. 104). The record for S. Perths. (Dalglish, 1901) applies to two ♀♀, and so must presumably also be transferred to the commoner species.

The occurrence of the species in certain other vice-counties is probable, but where records exist these require confirmation, *e.g.* E. Sussex, Haywards Heath (Morice) (Saunders, 1905); Suffolk, E., Lowestoft (Morice) (Saunders, 1896), and other localities (Morley, 1935); Merioneth, Towyn (Nevinson, 1900).

The following published records have been found to be based on incorrect identifications. Suffolk W., Tostock (Tuck) (Saunders, 1896; Morley, 1899): specimens in coll. Brit. Mus., 4 ♂♂ and 16 ♀♀, are all *trivialis*. Glos., W., Wotton (see above). Hereford, Tarrington, 1 ♀ (Yerbury) (Saunders, 1903;

Hallett, 1934): this specimen, in coll. Brit. Mus., is *trivialis*. Yorks, M.W., Roundhay and Collingham (Bradley) (Fordham, 1930): 4 ♀♀ in coll. R.C.L.P. are all *trivialis*. Sutherland, Golspie (Yerbury), 1 ♀ (Saunders, 1900). S. Kerry, Waterville, July 1901, 1 ♀ (Saunders, 1902; bracketed as doubtful by Stelfox, 1927): this specimen, in addition to the ♀ recorded as '*gibbus*,' is *trivialis*.

Among other published records are some which are almost certainly incorrect, and others for which no confirmation has been obtained. Clark (1906 *a* and *b*) gives one record of the male from the west of Cornwall, but this may be open to question. Altogether 24 ♂♂ and 53 ♀♀ have been examined from the county, mostly from sandy localities on the coast, but no *unguicularis* was found among them.

In review, the distribution of *unguicularis* appears to be fairly extensive in Great Britain, but the species is clearly more localized to sandy habitats than is *trivialis*. It is only at all common on certain coast sandhills, *e.g.* Glamorgan, Hayling Island, and Deal; on the Bagshot Sands of Surrey, S. Hants., and Dorset; and a few other sand formations, such as the Brecks of W. Suffolk. It ranges to some extent into more varied habitats, but is then generally much scarcer than *trivialis*. It may, however, be expected to occur as a rarity in other areas than those from which it is definitely known. It appears to spread further up on the west coast than on the east, reaching as far as S.W. Scotland (though confirmation of the single Scottish record is rather desirable). Its apparent absence, or at most extreme scarcity, in Devon and Cornwall is noteworthy; the gap in its distribution thus produced goes far towards the separation of its range into two sections, a south-eastern and a western — a process which is carried further in certain other aculeates which frequent sand-dunes in the west.

P. wesmaeli Thoms.

This is the scarcest and most localized of the three species, being apparently confined to certain coast sandhills, and, in still smaller numbers, to the Bagshot Sands areas of Surrey, S. Hants., and S.E. Dorset. Specimens have been confirmed from the following vice-counties.

Dorset: South Haven Peninsula, mostly on blown sand strata, but also on the Bagshot Sand, 5 ♂♂ and 3 ♀♀ (coll. G.M.S.); Studland (probably the above locality), 2 ♂♂ (Morice) (coll. Oxford Mus.); Moreton Heath, 1 ♀ (coll. G.M.S.).

S. Hants: New Forest, 1 ♂ and 1 ♀ (coll. R. C. L. Perkins); Beaulieu, 1 ♀ (coll. A. H. Hamm).

E. Kent: Deal, 1 ♂ (coll. Norwich Mus.), 1 ♂ (Morice) (coll. Oxford Mus.), 1 ♀ (Saunders) (coll. Brit. Mus.).

Surrey: Bagshot Sands district: Woking, 1 ♂ and 1 ♀ (Saunders) (coll. Brit. Mus.), 1 ♂ (Nevinson) (coll. Oxford Mus.); Horsell, 1 ♀ (R. J. Champion) (coll. Oxford Mus.); Chobham, 3 ♂♂ (Saunders) (colls. Brit. Mus. and Oxford Mus.), 1 ♂ and 1 ♀ (Arnold) (colls. Nevinson and Perkins, Oxford Mus.); Oxshott, 2 ♀♀ (coll. O. W. Richards), 1 ♀ (coll. A. H. Hamm).

Berks.: Bagshot Sands of S.E.: Wellington College, 1 ♂ (coll. A. H. Hamm).

Glamorgan: coast sandhills: Porthcawl, 9 ♂♂ (Hallett) (coll. Cardiff Mus.), 1 ♂ (Hallett) (coll. Perkins, Oxford Mus.), 1 ♂ (Yerbury) (coll. Brit. Mus.); Gower, 1 ♀ (D. Sharp) (coll. Camb. Mus.); 'Glamorgan sandhills,' 1 ♂ (coll. R. C. L. Perkins).

Carnarvon: Abersoch, 1 ♂ (Nevinson) (coll. Oxford Mus.); Llanfairfechen, 1 ♀ (coll. Brit. Mus.).

Cheshire: Wallasey, 1 ♀ (Arnold) (col. R.C.L.P., Oxford Mus.).

The following published records for additional localities, presumably based on captures of the male since females have been indeterminable, may be accepted. Hants. S.: Bournemouth (Saunders, 1896). Essex, N.: Colchester (Saunders, 1896; W. Harwood, 1903).

The localization has thus been carried a step further than in *unguicularis*.

Distribution in Relation to Habitat.

It has already been observed that *trivialis* is the most widely spread of the three species, being known from a larger number of districts; that *unguicularis* is localized to fewer districts, in which the strata are predominately sandy; and that *wesmaeli*, while occurring in nearly as many districts as the preceding, is yet more localized within them. The distribution of the specimens in the whole material examined is set out in Table II.

The relation to habitat can be examined more precisely if it is investigated within the confines of a limited area. South Dorset lends itself particularly to a study of this kind, owing to the rather exceptional variety in its geological strata and ecological settings. The results so far available from this area are entirely comparable with the picture obtained from Britain as a whole, and are worth summarizing. *P. trivialis* has been found in most localities in which collections have been made, though

TABLE II.

NUMBER OF SPECIMENS EXAMINED GROUPED UNDER DISTRICTS.

District	*P. trivialis* ♀	*P. trivialis* ♂	*P. unguicularis* ♀	*P. unguicularis* ♂	*P. wesmaëli* ♀	*P. wesmaëli* ♂
Surrey: Bagshot Sands localities	35	20	31	11	6	6
Kent E.: Deal (coast sandhills)	2	–	11	10	1	2
Kent, Surrey, Sussex: other localities	12	2	–	–	–	–
Bucks. and Middlesex	18	6	–	–	–	–
East coast: Essex N. (E.), Suffolk E., Norfolk E. ...	12	3	1*	1*	–	–
Suffolk W.: Brecks	8	2	4	–	–	–
Suffolk W.: Bury St. Edmund	16	4	–	–	–	–
Cambs., Hunts., Northants. ..	6	–	–	–	–	–
Berks. (S.E.): Bagshot Sands area	1	–	–	–	–	1
Berks. (N.)	9	–	5	1	–	–
Oxon	13	1	1	–	–	–
Hants. S.: Hayling Island ...	2	2	1	5	–	–
Hants. S.: New Forest (Tertiary Sands)	27	16	6	3	2	1
Isle of Wight	2	3	–	–	–	–
Dorset (S.E.): Bagshot Sands, etc.	27	11	25	10	4	7
Dorset: other localities ...	10	8	1	–	–	–
Devon S.	58	31	–	–	–	–
Devon N.	4	–	–	–	–	–
Cornwall and Scilly	62	25	–	–	–	–
Somerset N. and Wilts. N. ...	2	3	–	–	–	–
Glos. W.: Wotton-under-Edge	22	9	–	–	–	–
Hereford	2	–	–	–	–	–
Glamorgan: coast sandhills ...	7	3	9	6	1	11
Glamorgan: other localities ...	8	4	2	1	–	–
N. Wales, Cheshire, & S. Lancs.: coastal localities	15	3	3	–	2	1
Cheshire; inland	1	–	–	1	–	–
Notts.	1	–	–	–	–	–
Yorks.: N.E., N.W., M.W. ..	5	2	–	–	–	–
Scotland: Highlands	1	2	–	–	–	–
Ireland: E. and S. coasts ...	7	5	–	–	–	–
	395	165	100	49	16	29
No locality data ...	48	20	5	2	1	2

* Bridgman's specimens: presumably E. Norfolk.

it is clearly much restricted in well cultivated areas, particularly on heavy clay. Localities include coast undercliffs (Chideock, Charmouth, Lyme Regis), wooded areas on Upper Greensand strata (Powerstock Common, Glanvilles Wootton), broken ground on the stony Portland and Purbeck beds (Portland), exposed elevations on chalk ridges where these are capped with deposits of sandy gravel (Ridgeway Hill), sandy alluvium of the Wey estuary (Radipole Lake), settled blown sand on the edge of the Chesil Beach, and various localities on the Eocene beds of S.E. Dorset. To the westward, in S. Devon, several additional types of habitat presented are also colonized, *e.g.* bare ground on exposed turfy cliff slopes, exposures of soft slate and shale, granite sand on the slopes of Dartmoor, etc. The much more restricted nature of the habitats of *P. unguicularis* is evident from the localities given above (p. 105). As regards the Eocene beds of S.E. Dorset, *trivialis* is still the prevalent species on the Reading and London beds, which are clays with varying admixtures of sand, and which support much woodland. On the Bagshot Sands *trivialis* still appears more frequent on the edges of cultivated patches, grassy banks, etc., where the vegetation is other than that of heathland; but on the heathland proper (in sandpits, on banks, at sand exposures on the open heath, and sandy turf enclosures) *unguicularis* becomes rather the commoner of the two. Lastly, where dunes of blown sand border the Bagshot Sands, as at South Haven Peninsula, both species occur, *unguicularis* being the more frequent. *P. wesmaeli* appears on the Bagshot Sands, but is scarce: it only occurs at all freely, in favourable seasons, on the blown sand area (heather dune and marram dune) of South Haven.

The data available from other parts of Britain indicate a similar state of affairs. Mr. Hallett has kindly sent particulars of the localities in Glamorgan. Here *P. wesmaeli* is known from certain coast sandhills; *P. unguicularis* from coast sandhills, but also from at least three localities on outcrops of carboniferous limestone with overlying red marly soil (two of these, Cwyrt-yr-ala and Castell Coch, support woodland vegetation, and a third, Swanbridge, is rather sandy); *P. trivialis* from both the above habitats, and, in addition, from more inland areas on more elevated ground, *e.g.* Welsh St. Donats, where there is heather moorland. In this area *unguicularis* is not so restricted in comparison with *trivialis*, as it appears to be in the south and east of England.

PERIOD OF EMERGENCE.

A summary of the data of all fully dated specimens examined* is given in Table III. The dates are grouped into five-day

* A few records of the dates of males, supplied on reliable authority, are also included.

periods, the middle date of the period being given in the first column. The figures in other columns give the numbers of specimens of each species, the sexes separately, for each five-day period. Table IV gives total numbers for each month, for which many additional specimens are available.

TABLE III.

Frequencies of Dates of Capture.

(For further explanation see text.)

	P. trivialis		*P. unguicularis*		*P. wesmaeli*	
	♂	♀	♂	♀	♂	♀
May 4 ...	–	–	–	–	–	–
,, 9 ...	2	–	–	–	–	–
,, 14 ...	1	–	–	–	–	–
,, 19 ...	3	1	–	–	–	–
,, 24 ...	9	3	–	–	–	–
,, 29 ...	5	–	10	6	–	–
June 3 ...	11	6	–	–	–	1
,, 8 ...	9	8	1	2	1	–
,, 13 ...	7	9	–	1	1	–
,, 18 ...	7	9	2	2	1	–
,, 23 ...	2	8	–	1	4	–
,, 28 ...	1	6	–	3	2	1
July 3 ...	4	6	1	–	–	–
,, 8 ...	1	10	–	2	2	1
,, 13 ...	5	8	1	5	–	–
,, 18 ...	9	13	6	3	1	1
,, 23 ...	5	5	3	6	2	–
,, 28 ...	6	14	1	3	–	2
Aug. 2 ...	4	14	–	3	–	–
,, 7 ...	5	17	2	4	2	–
,, 12 ...	6	19	–	5	–	2
,, 17 ...	–	10	1	–	–	1
,, 22 ...	–	19	1	2	–	–
,, 27 ...	–	10	–	4	–	1
Sept. 1 ...	2	12	1	2	–	–
,, 6 ...	1	12	–	2	–	–
,, 11 ...	–	5	–	1	–	1
,, 16 ...	–	8	–	–	–	–
,, 21 ...	–	–	–	–	–	–
,, 26 ...	–	1	–	–	–	–
Oct. 1 ...	–	2	–	–	–	–
,, 3 ...	–	3	–	–	–	–
Total	105	238	30	57	16	11

TABLE IV.

FREQUENCIES OF CAPTURES PER MONTH.

	P. trivialis		*P. unguicularis*		*P. wesmaeli*	
	♂	♀	♂	♀	♂	♀
May ...	28	5	10	7	–	1
June ...	45	58	10	13	10	2
July ...	47	94	14	26	11	6
August ...	22	143	12	38	4	5
September ..	4	59	1	8	–	1
October ...	–	4	–	–	–	–
Total	146	363	47	92	25	15

P. trivialis.

The species normally emerges during the last ten days of May, when males predominate. The first appearance, however, appears to vary considerably with the season or with the exposure of the locality. The earliest dates for the male are 7 May (Mill Hill, Middlesex, *teste* K. M. Guichard) and 8 May (Plym valley, S. Devon); for the female, 19 May (Shepstor, S. Devon, 1940). The species is on the wing for the rest of the season, more females surviving into the early autumn than males. The latest dates are 7 Sept. for the male and 7 Oct. for the female. The monthly totals given in Table IV show a maximum for the male in June and July, and for the female in August.

Richards and Hamm (1939) have pointed out that there is no positive record that any British *Pompilus,* with the possible exception of *P. plumbeus* F., has more than one complete generation a year. If the present species has no more than one brood, then emergence must be 'staggered' over a surprisingly long period. Though no decisive proof can be provided, the data that have been examined, together with the experience gained in collecting these wasps over a period of years, indicate that, at least in the southern half of Great Britain, there are normally two broods—perhaps even sometimes three. The best indication of brood hatches may be expected to come from the males: these have probably a shorter span of life than the females, and when freshly emerged are liable to be noticed in some numbers over the ground from which they have hatched. If one brood normally occurs, an indication of more than one mode might be shown in the series of five-day period frequencies given in Table III. Inspection shows that there is in fact a marked indication of one peak at end-May to mid-June, and another from mid-July to early August. If the only seven records from Yorks., Scotland, and Ireland are deducted, leaving simply records for

the southern half of England and S. Wales, the gap between the modes is more pronounced.* I have found in Dorset that it is usual for freshly emerged males to appear from mid-July to the end of the month, after a scarcity in the latter part of June and early July. The occurrence of the species on a sandy cliff in E. Cornwall, visited on several occasions in 1939, again indicated two broods: males were numerous at the end of May, disappearing before early July, and re-appearing early in August. The distribution of the female frequencies in Table III shows no secondary peaks; on the other hand, it is not incompatible with the view that two broods occur, and the maximum reached during July and August may well be interpreted as the result of the appearance of a second brood more numerous than the first.

P. unguicularis.

This species appears at the end of May or early June, probably on the average only a week or two later than *trivialis*. In 1939, on 27 May, Mr. K. M. Guichard captured a series of both sexes on Deal sandhills. On Dorset heaths both sexes normally appear during the first half of June. Though the data are much more scanty than for *trivialis* (Tables III and IV), its distribution through the season appears to be similar. Table IV shows a maximum for the male in July and for the female in August. On the Dorset heaths evidence has been obtained that there are two broods in the season, a second hatch of males emerging in the latter half of July.

P. wesmaeli.

The available data indicates that this species emerges at much the same time as the last, but is 'over' earlier in the season. 21 out of 25 records of the male are for the months of June or July, and 9 out of 15 records of the female from May to July. The mid-summer seasonal distribution, which contrasts somewhat with that of the two previous species, is probably due to the fact that *wesmaeli* is single-brooded. The capture of a worn ♀ in Sept., 1938, at South Haven, Dorset, was accompanied by other abnormally late captures (*e.g. Chrysis succincta* L.), and is attributable to the exceptional weather of that season.

Other Aspects of Biology.

The available data on the nesting habits, prey, behaviour, etc., may be found in the survey of the biology of the family recently published by Richards and Hamm (1939), to which there is little to add. Records of reproductive behaviour of course suffer from the uncertainty as to which species was involved.

* The figures for the periods 29 May to 18 July become 5, 9, 9, 7, 6, 1, 1, 2, 0, 5, 9.

The British records of prey are all given under *trivialis* (*loc. cit.*, pp. 82-83), and of these three (namely the Scilly, Portland, and Bigbury records) can now be stated to apply to this species with certainty. The three spiders involved—*Drassodes lapidosus* (Walck.), *Lycosa* sp., and *Clubiona* sp.—belong to three separate families (Drassidae, Lycosidae, and Clubionidae respectively). A fourth (Pisauridae) is involved in the single new record which can be given:

E. Cornwall: Rock, near St. Minver, 30.vii.39 (G.M.S.), a very young *Pisaura listeri* (Scop.) (det. Dr. A. R. Jackson).

Richards and Hamm (*loc. cit.*) suspect that one of the *Pompilus* species here considered tends to specialize in spiders of another family, the Thomisidae, and that most Thomisid records refer to that one particular species, whatever it is. It was therefore of especial interest to find that the wasp concerned in the Thomisid *Xysticus* sp. record for Tubney, 4 Sept. 1917 (A.H.H.) (specimen in the Oxford University Museum collection) belonged to *unguicularis*. This is the only British record of prey for that species so far available. I have on two occasions seen what proved to be an *unguicularis* ♀ transporting spider prey, one to a burrow in a sandy bank, and the other in a sand pit. It is unlikely that the nesting habits are very different from those of *trivialis*. Since *unguicularis* has weaker claws, one might anticipate that it would show preference for light sandy ground, as is actually found (p. 110). *P. wesmaeli*, which is even more restricted to such ground, has similar weak claws. For this latter species no observations on behaviour in this country appear to exist, and those recorded on the continent (*loc. cit.*, p. 83) may involve doubtful identifications.

To the few recorded predatory enemies, *Cicindela sylvatica* may be added: a female *P. unguicularis* was taken in the jaws of one of these tiger beetles on Godlingston Heath, Dorset, 12.vii.33.

The three species here considered are usually seen running or making short flights over the ground, at exposures of sand and other light soils, which may be completely bare, or covered with a sparse growth of grasses or other vegetation, but normally not on the steep slopes of cuttings. The females hunt at the base of tufts of vegetation. Neither the males nor females appear to spend much time at flowers. The following are the only records of captures at flowers that have come to my notice:

Daucus: *P. trivialis*, 11 ♀♀, Slough, Bucks (O. W. Richards); 1 ♀, Moreton, Dorset; 1 ♀, St. Minver, E. Cornwall, 1939.

Oenanthe: *P. trivialis*, 1 ♀, Dorset (C. D. Day).

Angelica: *P. trivialis*, 3 ♀♀, Dorset; 1 ♂, Slough, Bucks. (O. W. Richards).

Euphorbia: *P. unguicularis*. Both sexes recorded by H. P. Jones (1926) as visiting this plant freely in the New Forest. (But three ♀♀ sent me by Mr. Jones, supposed to contain at least one of the captures at *Euphorbia*, were *trivialis*.)

Achillea: *P. unguicularis*, 1 ♂, Arran (Dalglish, 1901).

Potentilla: *P. trivialis*, 1 ♂, Dorset.

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APPENDIX

I. SUMMARY OF DATA OF MEASUREMENTS.

The results of the quantitative data secured are shown in the accompanying table (Table V). These refer to the same 48 specimens of *trivialis*, 24 of *unguicularis*, and 6 of *wesmaeli*. The distribution of these specimens according to localities is as follows:

P. trivialis: Scilly Is. 6, W. Cornwall 1, E. Cornwall 2, S. Devon 5, N. Devon 1, Dorset 19, I. of Wight 1, W. Kent 1, Surrey 3, Bucks. 5, Cambs. 1, W. Glos. 3. *P. unguicularis*: Dorset 19, Surrey 3, W. Suffolk 1, S. Lancs. 1. *P. wesmaeli*: Dorset 4, Surrey 2.

The samples are thus far from random for the British Isles, and heavily weighted for Dorset and other southern counties. Consequently no stress is laid on the exact values of the means. It is possible that these might differ slightly in different parts of Britain. But no indication has been found that, if any such difference occurs, it is of any appreciable dimension. Judgments made by eye indicate that the species show a similar average condition and degree of variation in all parts of their range in Britain.

The original measurements on the head and wings were made in micrometer units of 0·0087 mm. Those on the postnotum were made under somewhat higher magnification in units of 0·0062 mm. The ratios could thus be calculated with considerably greater accuracy than the ·05 interval in which they

TABLE V. Frequency Distributions for Characters Measured.

																							Total	Mean	Sq. root of variance
Ratio POL/OOL	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60											
trivialis	–	–	–	–	–	4	6	17	6	10	2	2	1	–									48	1·332	0·079
unguicularis	–	5	10	8	–	1	–	–	–	–	–	–	–	–									24	1·060	0·050
wesmaeli	–	–	2	–	1	3	–	–	–	–	–	–	–	–									6	1·15	—
Ratio E′/T	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55	1.60	1.65	1.70	1.75	1.80	1.85	1.90	1.95	2.00			
trivialis	–	–	–	–	–	–	–	1	2	–	1	3	4	6	8	6	8	4	1	–	3	1	48	1·668	0·150
unguicularis	–	1	6	7	4	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	24	1·131	0·093
wesmaeli	–	–	1	1	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	1·15	—
Ratio ½F/E″	0.90	0.95	1.00	1.05	1.10	1.15	1.20	1.25	1.30	1.35	1.40	1.45	1.50	1.55											
trivialis	11	15	12	5	3	1	1	–	–	–	–	–	–	–									48	0·978	0·067
unguicularis	–	–	–	–	–	–	–	7	7	5	2	1	2	–									24	1·330	0·074
wesmaeli	–	–	–	–	–	–	–	2	1	2	–	1	–	–									6	1·32	—
Ratio Pn/Ps	0.45	0.50	0.55	0.60	0.65	0.70	0.75	0.80	0.85	0.90	0.95	1.00	1.05	1.10	1.15										
trivialis	–	–	1	1	3	10	12	7	7	3	2	–	1	–	1								48	0·78	0·109
unguicularis	–	5	6	10	3	–	–	–	–	–	–	–	–	–	–								24	0·573	0·047
wesmaeli	–	–	–	2	1	3	–	–	–	–	–	–	–	–	–								6	0·66	—
Width of Head (across face) (mm.)	1.64	1.73	1.82	1.91	2.00	2.09	2.18	2.27	2.36																
trivialis	–	–	5	9	12	7	5	7	3														48	2·03	—
unguicularis	4	5	4	5	2	2	–	2	–														24	1·87	—
wesmaeli	1	1	2	1	–	–	–	–	–														6	1·79*ca.*	—
Length *xyz* (mm.)	2.40	2.60	2.80	3.00	3.20	3.40	3.60	3.80	4.00																
unguicularis	–	4	5	6	4	2	2	–	1														24	3·15	—
wesmaeli	–	–	3	2	1	–	–	–	–														6	2·95*ca.*	—
Ratio *xy*/*yz*	0.84	0.87	0.90	0.93	0.96	0.99	1.02	1.05	1.08	1.11	1.14	1.17	1.20												
unguicularis	–	–	–	–	2	1	–	4	5	7	3	2	–										24	1·084	0·058
wesmaeli	–	2	2	1	–	–	–	–	–	–	–	–	–										6	0·91	—

are grouped in the table. Where means of the two sides of the body could be taken individual values can easily be given correct to the nearest second place of decimal.

In Table V the Arithmetic Mean and the square root of the Variance are given for each set of figures. The latter statistic is equivalent to the standard deviation when the distribution of the group is normal, or approximately so. If required, the standard errors can be simply derived from the data given, by the usual methods.

II. Inferences from Correlation Tests.

The remarks which are included in this section on certain information which can be derived from the quantitative data may be of interest in showing how elementary statistics may be brought to the aid of taxonomic studies.

Tests were made for correlations between the characters measured. The number of specimens from which data was secured is rather small for this purpose, but the 48 specimens of *trivialis* are adequate to show up strong or moderate correlations, and the 24 of *unguicularis* at least adequate to show up correlations above ·5 or ·6. The few *wesmaeli* have to be ignored.

For *trivialis* there are four different ratio values—POL/OOL, E′/T, $\frac{1}{2}$F/E″, and Pn/Ps — and one size-index value, the width of the front of the head. Tested against the last, each of the first three ratios fails to show any signs of correlation; while Pn/Ps shows a weak inverse correlation with the head-width ($-$ ·28 $\pm$ ·133), possibly not significant, and certainly of no practical importance. The four characters in question may thus be regarded as independent of the size of the specimens.

In considering the possibility of correlation between the four ratio values, it must be noted that the first three apply to dimensions of the head, and each might be affected similarly by, for example, variation in the size of the eye. Consequently it would not be surprising to find marked correlation among them (this would be negative where $\frac{1}{2}$F/E″ is involved, since the eye dimension is here denominator, whereas in the other two it is numerator). Actually only one comparison shows any correlation at all — that between E′/T and $\frac{1}{2}$F/E″, for which the value is $-$ ·314 $\pm$ ·131. These two ratios apply to characters which are the most closely connected, one involving the width of the eye in front view and the other the width in side view. The other two comparisons show no significant correlation. Thus the temple-width and face-width are largely independent, while the spacing of the posterior ocelli is completely independent of both. The justification for treating these ratios as separate characters is thus confirmed.

When the ratio Pn/Ps is compared with the head ratios, the results indicate that it is possibly not completely independent of them, the values obtained being: with POL/OOL, $+\cdot17 \pm \cdot140$; with E′/T, $+\cdot26 \pm \cdot134$; with $\frac{1}{2}$F/E″, $-\cdot15 \pm \cdot140$. However, any actual correlation must be small, and the independence of this character is quite sufficient for all practical purposes.

For *unguicularis* an additional ratio, xy/yz in the wing, and an additional size-index, $xy+yz$, are available; but owing to the comparatively small number of specimens measured only strong correlations can be looked for. As in *trivialis*, none of the head ratios shows any correlation with size, while a small inverse correlation may again exist for Pn/Ps ($-\cdot23 \pm \cdot194$, which in itself is not significant). Again, then, these ratios can be regarded as independent of the size of the specimen. It is otherwise, however, with the wing ratio xy/yz. This shows a decided positive correlation with the width of the face, and a stronger correlation, $+\cdot79 \pm \cdot079$, with the size of the wing, as represented by $xy+yz$ (see also Fig. 10). This ratio thus increases somewhat with the size of the specimen. Consideration of this fact is necessary to bring out fully the difference between *unguicularis* and *wesmaeli* (p. 98).

Comparison of the five ratios among themselves show no correlations of any magnitude, confirming that the characters can be treated as independent of each other. Possible minor correlations are again indicated between E′/T and $\frac{1}{2}$F/E″ ($-\cdot26 \pm \cdot195$), and between Pn/Ps and E′/T ($+\cdot34 \pm \cdot185$).

Attention may be called to the contrast between the *intra*-specific independence of the characters dealt with, and the *inter*-specific correlation which follows from the fact that they jointly serve to define the difference between *trivialis* and *unguicularis*. If, for any of the characters, the ratio values for the two species are pooled, and fresh comparisons made, in every case a strong correlation may be expected, and is in fact found. For example, the results for the comparison between POL/OOL and E′/T are as follows:

Both species combined, correlation	$+\cdot79$	$\pm \cdot045$
Trivialis alone, ,,	$+\cdot195$	$\pm \cdot140$
Unguicularis alone, ,,	$-\cdot22$	$\pm \cdot200$

It is here probable that there is no intraspecific correlation at all; but even if small ones exist they are evidently of quite a different order from the high correlation when the two species are combined. A complete contrast also is shown by the comparison between POL/OOL and $\frac{1}{2}$F/E″:

Both species combined, correlation	$-\cdot80$	$\pm \cdot043$
Trivialis alone, ,,	$-\cdot06$	$\pm \cdot145$
Unguicularis alone, ,,	$+\cdot40$	$\pm \cdot175$

The least contrast is shown in the comparison between E′/T and ½F/E″:

Both species combined, correlation		− ·845 ± ·034
Trivialis alone,	,,	− ·314 ± ·131
Unguicularis alone,	,,	− ·26 ± ·195

But even here the characters are to a large extent independent intraspecifically.

The correlations involving Pn/Ps behave in a similar way. Thus, when tested with POL/OOL, the results are:

Both species combined, correlation		+ ·716 ± ·059
Trivialis alone,	,,	+ ·17 ± ·140
Unguicularis alone,	,,	+ ·03 ± ·210

It will be recalled that in this character there is considerable overlapping between the two species, yet the correlation shown by the combined values is high.

For any of the combinations of pairs of characters, lack of intraspecific correlation means that if a specimen happens to diverge far from the mean condition of the species in one of the characters, it is no more likely than any other specimen to diverge to the same extent and in the same direction in respect to the other character. But the divergence of one species from the other involves both characters at the same time, and so includes an element which cannot be detected if the variation within an assemblage composed entirely of one of the species is examined. This can only imply that a radical diversity exists between the two assemblages (which in this case from other evidence we have been assigning to two distinct species). If it had happened that doubt had existed whether one or two species were present, and if there had been only one pair of characters known by which the two assemblages could be distinguished, this consideration would have provided sufficient grounds for regarding them truly distinct.

III. Possibility of combining Characters.

The principle on which the females of *trivialis* and *unguicularis* are separated is that of taking the balance of several characters, none of which is quite diagnostic. Two or more of these characters might theoretically be combined, and, assuming they are not correlated (as has been shown above), compose a single character on which the two species might be absolutely separable. If the characters are expressed numerically, combining the values of two or more is quite practicable, and ratio values particularly lend themselves to this treatment.

In combining two such values, it is clearly immaterial what their absolute size may be, but it is important that the units in which they are expressed should be such that the standard deviation (or, more strictly, the variance) of the two characters is as nearly identical as possible. If this is not so, one character is unduly weighted, its deviations not being adequately offset by those of the other.

The effect of combining the three head ratios, POL/OOL, E′/T, and $\frac{1}{2}$F/E″, may be tested. Let these be designated respectively *a*, *b*, and *c*. E′/T has a greater range of variation than the other two, and must consequently be proportionately reduced. Approximately equal weight is given to each of the three characters in the combination $a + \frac{1}{2}b - c$. If the value for this is calculated for each specimen and treated as a single characteristic, the following results are obtained:

	Mean value of $a+\frac{1}{2}b-c$	Range	Standard deviation	Calculated stndrd. deviation
trivialis	1·190	0·80—1·44	0·140	0·131 ± 0·013
unguicularis	0·299	0·14—0·48	0·085	0·100 ± 0·0145

There is thus a considerable gap between the ranges of the two species. The difference between the two means, 0·891, is over five times the combined standard deviations (0·166). Intermediates would thus occur in an insignificantly small proportion of specimens, so that this characteristic is virtually diagnostic. The values for the standard deviations obtained are in good agreement with the expected standard deviation calculated on the assumption that the three component characters are independent of each other.

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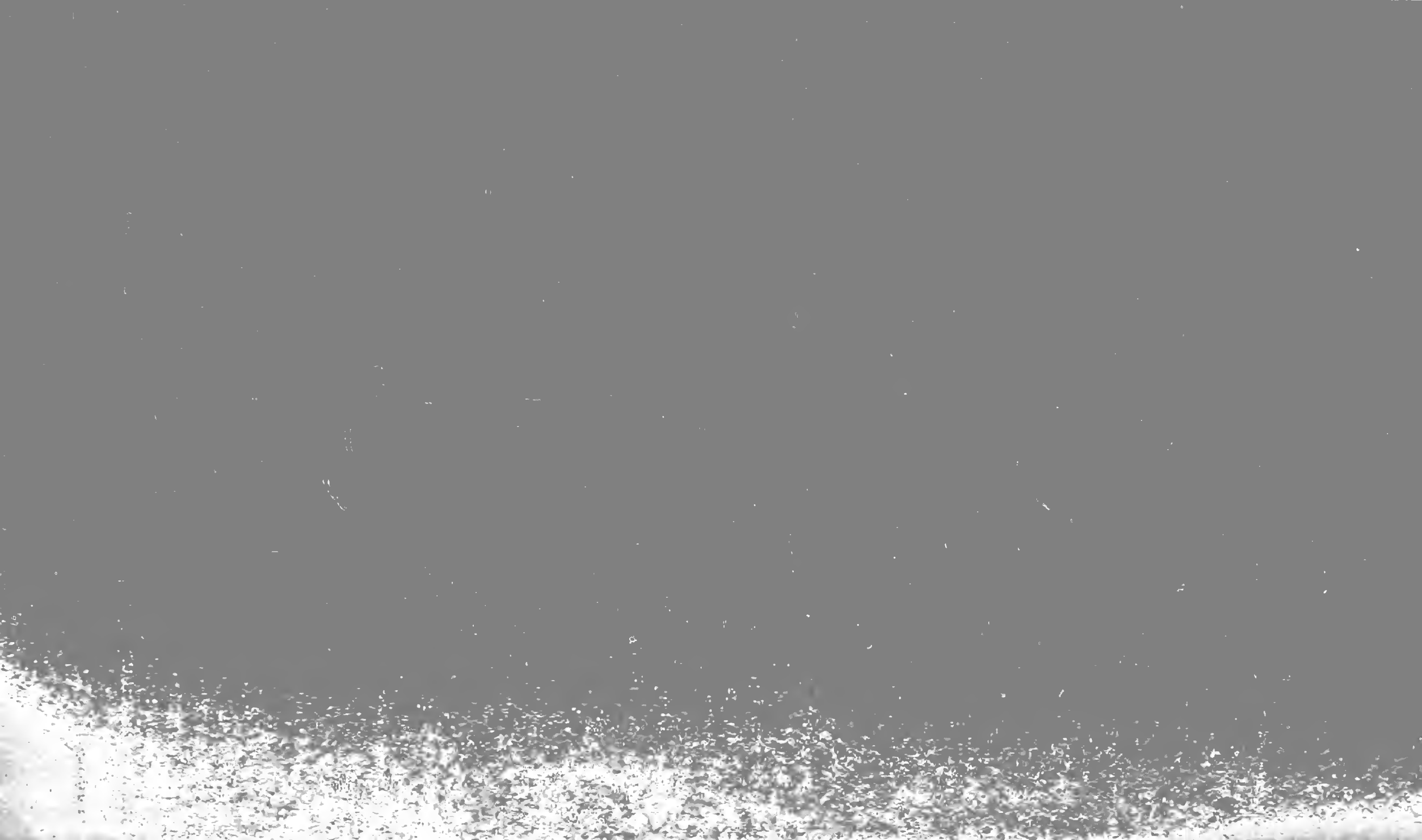

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